



Data Paper

Vertical distribution of arthropod assemblages in native and exotic forests of Terceira Island (Azores, Portugal)

Sébastien Lhoumeau[‡], Abrão Leite[§], Laurine Parmentier[‡], Clémence Massard[‡], Martha Vounatsi[¶], Georgery Lucie[#], Paulo A. V. Borges^{‡,*,«}

[‡] University of the Azores, cE3c- Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group, CHANGE – Global Change and Sustainability Institute, School of Agricultural and Environmental Sciences, Rua Capitão João d'Ávila, Pico da Urze, 9700-042, Angra do Heroísmo, Azores, Portugal

[§] Rua Fernando Pessoa, nº99 R/C DTO 2765-483, Estoril, Portugal

[|] Mestrado em Gestão e Conservação da Natureza, University of the Azores Rua Capitão João d'Ávila, Pico da Urze 9700-042, Angra do Heroísmo, Azores, Portugal

[¶] Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of Athens, Athens, Greece

[#] UCLouvain - Unamur, Faculty of Biology, Louvain-La-Neuve, Belgium

[✱] IUCN SSC Atlantic Islands Invertebrate Specialist Group, Angra do Heroísmo, Azores, Portugal

[«] IUCN SSC Monitoring Specialist Group, Angra do Heroísmo, Azores, Portugal

Corresponding author: Sébastien Lhoumeau (seb.lhoumeau@gmail.com)

Academic editor: António O. Soares

Received: 28 Mar 2025 | Accepted: 05 May 2025 | Published: 20 May 2025

Citation: Lhoumeau S, Leite A, Parmentier L, Massard C, Vounatsi M, Lucie G, Borges PAV (2025) Vertical distribution of arthropod assemblages in native and exotic forests of Terceira Island (Azores, Portugal).

Biodiversity Data Journal 13: e154240. <https://doi.org/10.3897/BDJ.13.e154240>

Abstract

Background

In the summer of 2024, a study was conducted on Terceira Island in the Azores Archipelago, Portugal, aiming to characterise the vertical diversity and spatial distribution patterns of arthropods within native and exotic forest ecosystems. This study forms part of a broader research initiative designed to investigate how alterations in habitat structure influence the complexity and stability of arthropod food webs in Azorean forest habitats. By systematically sampling arthropods across multiple vertical strata—from forest floor to canopy the study aimed to generate detailed insights into the ecological dynamics governing biodiversity patterns and species interactions. Results from this monitoring will

contribute significantly to understanding the ecological impacts of forest composition and management strategies, ultimately providing information for conservation planning and habitat restoration efforts aimed at preserving arthropod diversity and ecological resilience in island ecosystems.

New information

The current dataset comprises identified terrestrial arthropods collected using SLAM (Sea, Land and Air Malaise) traps and Pitfall traps across diverse forest strata. A total of 32,797 specimens were collected from the Arachnida, Diplopoda, Chilopoda and Insecta classes. A total of 18,372 (56%) were identified at the species or subspecies level, including 12,745 adults and 5,627 juveniles for taxa, such as Araneae and Hemiptera due to the availability of reliable identification methods. The resulting dataset encompasses 150 species and 11 subspecies, distributed across 21 orders, 81 families and 148 genera.

Hemiptera emerged as the most abundant identified order, with a total of 7,697 recorded specimens and Coleoptera stood as the most taxonomically diverse, encompassing 19 distinct families and 50 species and sub-species. The ten most abundant species comprise predominantly endemic and native non-endemic species, with two exotic species detected amongst them.

This comprehensive dataset serves as a significant augmentation of the existing baseline knowledge concerning the diversity of Azorean arthropods, thereby facilitating the formulation of future long-term ecological comparisons. It offers valuable insights into the vertical distribution of species abundance within both native and exotic forests of the Azores.

Keywords

occurrence, specimen, Arthropoda, Azores, forest stratification, SLAM trap, Pitfall trap, sampling event

Introduction

Forests represent amongst the most structurally complex ecosystems on Earth (Pan et al. 2013, Ehbrecht et al. 2021), characterised by distinct vertical strata that support a wide range of biodiversity (Oliveira and Scheffers 2019). The vertical stratification of forests plays a crucial role in shaping species distributions, ecological interactions and resource availability (Laurans et al. 2014, Thiel et al. 2021, Basham et al. 2023). The different forest layers — ranging from the forest floor to the canopy — offer distinct environmental conditions, including variations in temperature, humidity, light availability and plant composition (Chen et al. 1999, De Frenne et al. 2019). Consequently, many forest-

dwelling organisms, including arthropods, exhibit strong vertical preferences and niche partitioning (Basset et al. 2003). However, despite the recognised importance of vertical stratification in forest ecology, studies on arthropod diversity across forest layers remain limited, especially in insular ecosystems (but see Costa et al. (2023)).

Arthropods are considered to be one of the most functionally diverse and ecologically significant animal groups. They play key roles in decomposition, pollination, herbivory, predation and soil aeration (Wong et al. 2019, Cardoso et al. 2020, Cardoso et al. 2024). Due to their sensitivity to habitat structure and environmental changes, arthropods are widely used as bioindicators of ecosystem health (Tsafack et al. 2023). Understanding their distribution across vertical forest layers can provide insights into species interactions, habitat specialisation and the effects of environmental disturbances on biodiversity. In island ecosystems, where species assemblages are often shaped by historical colonisation events, habitat fragmentation and the introduction of invasive species (Fernández-Palacios et al. 2021), investigating arthropod vertical stratification can be particularly valuable for conservation planning. Island ecosystems, such as those of the Azores (Portugal), exhibit unique biodiversity patterns, shaped by isolation, habitat heterogeneity and anthropogenic influences, making them valuable natural laboratories for ecological research and biodiversity management strategies (Mueller-Dombois 1992).

The Azorean forests, include both native and exotic forest types, each of which differs in terms of floristic composition, structural complexity and historical land use (Dias et al. 2004, Elias et al. 2016, Borges Silva et al. 2022). The native forests, which are dominated by endemic tree species, such as *Laurus azorica*, *Ilex azorica* and *Juniperus brevifolia*, represent remnants of the Pliocene/Pleistocene forests in Macaronesia (Kondraskov et al. 2015). These forests are distinguished by their notable levels of endemism and conservation importance, offering critical habitat for specialised arthropod species (Borges et al. 2022, Lhoumeau and Borges 2023). In contrast, exotic forests are characterised by the presence of the invasive species *Pittosporum undulatum*, along with other non-native vascular plants and are the result of deliberate afforestation for timber production and land management purposes (Dias et al. 2004, Borges Silva et al. 2017). As a consequence, they frequently exhibit a lack of structural and botanical diversity when compared to native forests, potentially influencing the composition and distribution of arthropod communities.

Given that many insular arthropods exhibit high levels of habitat specialisation and restricted dispersal abilities (Gillespie and Roderick 2002), their vertical distribution within forest strata could be influenced by both natural forest structure and anthropogenic modifications. Additionally, the replacement of native forests with exotic species may lead to changes in arthropod assemblages by altering microhabitat conditions, reducing resource availability and disrupting ecological interactions.

General description

Purpose: The present dataset encompasses terrestrial arthropods that have been collected using Pitfall traps and SLAM (Sea, Land, and Air Malaise) traps across a variety of forest strata. This dataset is the material result of sampling events that have been conducted within the framework of a project that aims to evaluate the impact of habitat structure change on arthropod food web complexity in Azorean forests. In particular, the study seeks to assess how changes in arthropod biodiversity are influenced by the structural complexity of forests.

Project description

Title: The impact of habitat structure change on arthropod food web complexity in Azorean forests.

Personnel: Paulo A. V. Borges, Sébastien Lhoumeau, Laurine Parmentier, Abrão Leite, Clémence Massard, Martha Vounatsi, Georgery Lucie

The project was conceived and is being led by Sébastien Lhoumeau and Paulo A.V. Borges.

Fieldwork (site selection and experimental setting): Sébastien Lhoumeau and Paulo A.V. Borges.

Fieldwork (authorisation): Licença N° 23/2024/DRAAC; ADENDA CCIR-RAA/2024/7.

Fieldwork: Sébastien Lhoumeau, Clémence Massard, Martha Vounatsi, Georgery Lucie and Paulo A.V. Borges.

Parataxonomists (Laboratory): Sébastien Lhoumeau, Laurine Parmentier, Abrão Leite, Clémence Massard, Martha Vounatsi, Georgery Lucie.

Taxonomists: Paulo A. V. Borges.

Arthropod Curation: Voucher specimen management was mainly undertaken by Sébastien Lhoumeau, Laurine Parmentier and Abrão Leite.

Darwin Core Databases: Sébastien Lhoumeau and Paulo A.V. Borges.

Study area description: The Azores constitute an isolated archipelago located in the northern part of the mid-Atlantic Ocean, approximately 1,400 kilometres west of mainland Portugal. Comprising nine volcanic islands — namely Corvo, Flores, Faial, Pico, São Jorge, Graciosa, Terceira, São Miguel and Santa Maria — the Archipelago extends across roughly 500 km in a west-northwest to east-southeast orientation. Santa Maria, with its age around 6 to 8 million years, is the most ancient island within the archipelago. In contrast, Pico, the youngest island, has an estimated age of around 0.19 million years (Florencio et al. 2021). The islands emerged through volcanic activity along the Mid-

Atlantic Ridge, a tectonic boundary zone, characterised by ongoing seismic and geothermal phenomena and most of the islands are relatively young (Florencio et al. 2021). This volcanic origin has endowed the Azorean Islands with rugged terrains, diverse habitats and unique ecological communities, which together contribute to their important unique biodiversity and biogeographic significance (Florencio et al. 2021, Borges et al. 2022).

During this project, the Island of Terceira (the third largest) was surveyed. Ten sampling plots were selected in areas of native vegetation, predominantly dominated by endemic species such as *Juniperus brevifolia*, *Erica azorica*, *Laurus azorica* and *Ilex azorica*, with currently some spread of invasive species like *Hedychium gardnerianum*. Ten additional plots were situated in secondary forests, predominantly characterised by *Pittosporum undulatum* and *Hedychium gardnerianum*, yet exhibiting indications of endemic and native ferns, such as *Dryopteris azorica* and *Diplazium caudatum*.

Design description: The experimental design comprised a 90-day sampling period, spanning from mid-June to mid-September 2024 (summer period), across all twenty sites. The sampling method employed was SLAM traps, with a maximum of three traps deployed at each site. In locations where feasible, these traps were positioned at varying heights within the forest, specifically at 0% (ground trap, hereafter GRD), 50% (understorey trap, UND) and 75% (canopy trap, CAN) of the maximum canopy height. In the event that the understorey trap was separated from the other two traps by less than 1 vertical metre, this trap was not set up.

Additionally, 14 Pitfall traps (hereafter EPI) were randomly set up at each site for a duration of 14 days, starting in July and concluding in August 2024.

Funding: Sebastien Lhoumeau was funded by the project "The impact of habitat structure change on arthropod food web complexity in Azorean forests" (PhD grant M3.1.a/F/012/2022).

Additional funding come for :

Portal da Biodiversidade dos Açores (2022-2023) - PO Azores Project - M1.1.A/INFRAEST CIENT/001/2022;

FCT-UIDB/00329/2020-2024 (Thematic Line 1 – integrated ecological assessment of environmental change on biodiversity) (2019-2024);

Science and Technology Foundation (FCT) - MACRISK-Trait-based prediction of extinction risk and invasiveness for Northern Macaronesian arthropods (FCT-PTDC/BIA-CBI/0625/2021).

Open access was funded by the project FCT-UID/00329/2025, Centre for Ecology, Evolution and Environmental Changes (CE3C).

Sampling methods

Description: A total of twenty 20 m x 20 m plots were sampled in one island from the Archipelago (Terceira). Ten of these plots were set up within the most well-preserved forests in this island, having limited human disturbance (Borges et al. 2017). The native forest is dominated by endemic vegetation, such as *Juniperus brevifolia*, *Erica azorica*, *Laurus azorica* and *Ilex azorica* (see Borges et al. (2017) for more details). Ten other plots are in secondary forests, which are dominated by exotic and invasive trees.

Sampling description: Passive flight interception SLAM traps (Sea, Land and Air Malaise trap, Fig. 1) were used to sample the plots, with three traps being set up at each plot at different height within the forest. Traps are 110 × 110 × 110 cm. In this type of trap, the trapped arthropods crawl up the mesh and then fall inside the sampling recipient (Borges et al. 2017). Each one is filled with propylene glycol (pure 1,2-PROPANODIOL) to kill the captured arthropods and conserve the sample between collections, enabling also the preservation of DNA for future genetic analysis. Although this protocol was developed to sample flying arthropods, by working as an extension of the tree, non-flying species, such as spiders, can also crawl into the trap (Borges et al. 2017), enhancing the range of groups that can be sampled by this technique. As a result, previous studies have used these traps to analyse diversity and abundance changes in the arthropod communities in Azores pristine forest sites (Matthews et al. 2019, Borges et al. 2020, Lhoumeau and Borges 2023). The traps samples were collected after three months in the studied sites.



Figure 1. [doi](#)

Picture of the set-up of the three SLAM traps within the exotic forest (site TER-EXO-T04) (Credit: Sébastien Lhoumeau).

We completed the sampling by using 14 passive Pitfall traps (Fig. 2) randomly distributed within the plots to sample the epigean fauna. Traps have a 5 cm opening diameter and

filled with ethylene glycol. Pitfall traps were collected after two weeks (14 nights) of continuous operation.



Figure 2. [doi](#)

Picture of a Pitfall trap set-up (the protective cover is removed) (Credit: Sébastien Lhoumeau).

Quality control: All sorted specimens were identified by a taxonomical expert, one of the authors P.A.V.B. and species taxonomic nomenclature and species colonisation status follows Borges et al. (2022).

Geographic coverage

Description: Terceira Island, Azores (Portugal), Fig. 3.

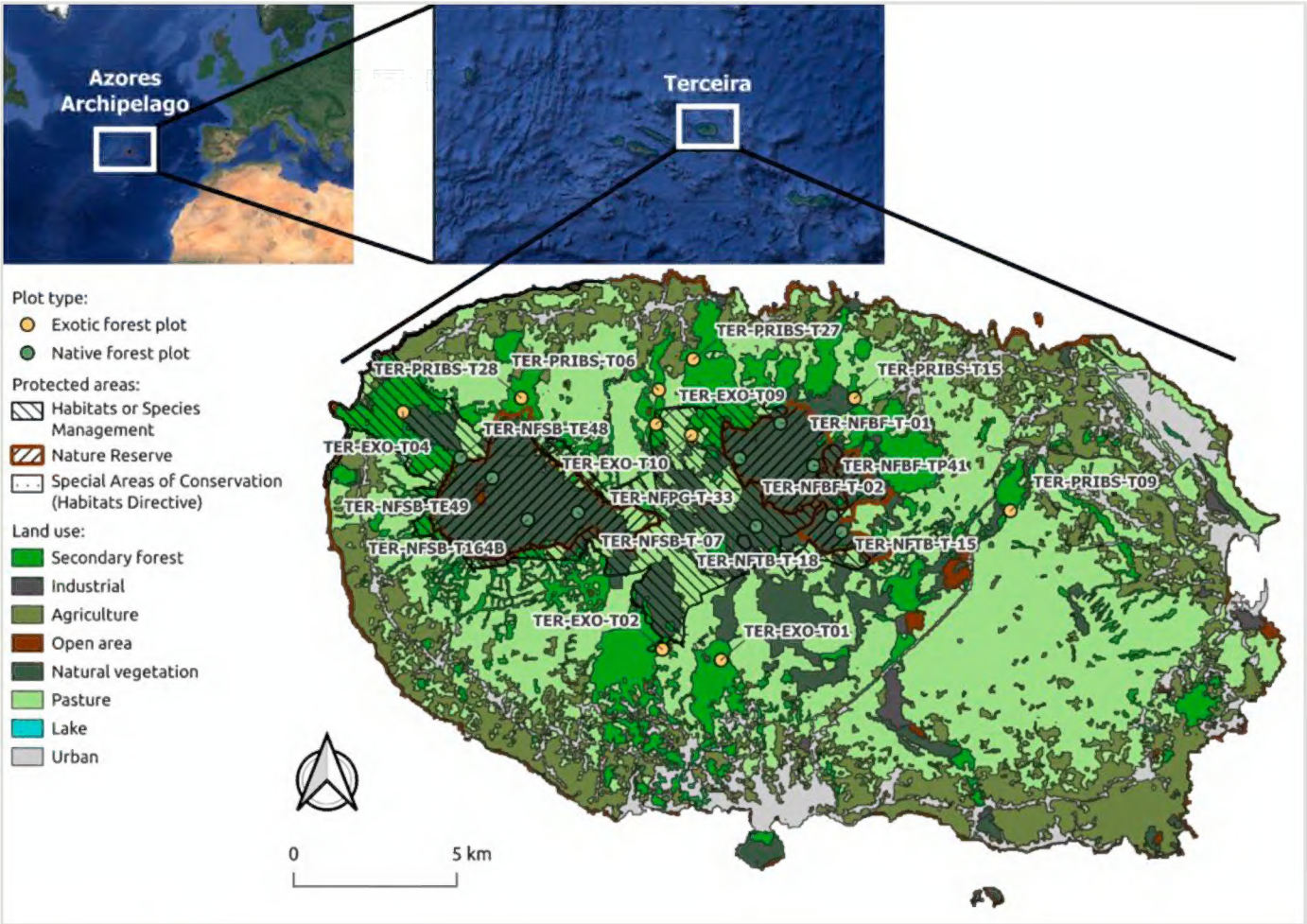


Figure 3. [doi](#)

Location of Terceira Island. For comprehensive details regarding the sampling sites, refer to Table 1. The protected areas data was sourced from UNEP-WCMC (2025), while the land-use data were provided by the [Azorean government](#).

Table 1.

List of the 20 sampled sites in Terceira.

Information about the habitat, location identifier, locality, decimal coordinates and elevation in metres are provided.

In the habitat, we classify the type of native forest based on Elias et al. (2016): (1) *Laurus* Submontane Forests, (2) *Juniperus-Ilex* Montane Forests, (3) *Juniperus* Montane Woodlands. Exotic forests are dominated by the invasive tree species *Pittosporum undulatum*.

Elevation data are sourced from OpenTopography (2013).

In locations indicated by the asterisk, only two SLAM traps were installed. The implementation of the understorey trap was rendered unfeasible due to the reduced canopy height.

Habitat type	Site code	Site name	Decimal longitude	Decimal latitude	Elevation above sea level (m)
Exotic forest	TER-EXO-T01	Mata do Estado	-27.24	38.697	425
Exotic forest	TER-EXO-T02	Matela	-27.26	38.7	394
Exotic forest	TER-EXO-T04	Serreta 400	-27.352	38.765	376

Habitat type	Site code	Site name	Decimal longitude	Decimal latitude	Elevation above sea level (m)
Exotic forest	TER-EXO-T09	Caparica Horses	-27.263	38.762	417
Exotic forest	TER-EXO-T10	Gruta do Balcões	-27.25	38.759	459
Exotic forest	TER-PRIBS-T06	Caparica	-27.262	38.771	336
Exotic forest	TER-PRIBS-T09	Fontinhas	-27.138	38.738	256
Exotic forest	TER-PRIBS-T15	Agualva	-27.193	38.769	367
Exotic forest	TER-PRIBS-T27	Gruta Chocolate	-27.249	38.779	271
Exotic forest	TER-PRIBS-T28	Pico Rachado	-27.31	38.769	461
Native forest (1)	TER-NFBF-T-01	Morro Assombrado	-27.219	38.762	680
Native forest (3)	TER-NFBF-T-02 (*)	Biscoito da Ferraria	-27.233	38.752	590
Native forest (3)	TER-NFBF-TP41	Pico Alto	-27.207	38.75	673
Native forest (2)	TER-NFPG-T-33	Pico Galhardo	-27.227	38.734	643
Native forest (2)	TER-NFSB-T-07	Lomba	-27.29	38.737	683
Native forest (3)	TER-NFSB-T164B	Santa Bárbara	-27.308	38.735	899
Native forest (3)	TER-NFSB-TE48	Lagoinha	-27.331	38.752	678
Native forest (3)	TER-NFSB-TE49 (*)	Lagoa do Pinheiro	-27.331	38.752	927
Native forest (1)	TER-NFTB-T-15	Terra Brava A	-27.201	38.736	637
Native forest (1)	TER-NFTB-T-18	Terra Brava B	-27.197	38.732	679

Coordinates: -27.04093 and -27.39698 Latitude; 38.81982 and 38.62170 Longitude.

Taxonomic coverage

Description: The following orders and class are covered:

Taxa included:

Rank	Scientific Name
kingdom	Animalia
phylum	Arthropoda
class	Insecta
class	Arachnida
class	Diplopoda
class	Chilopoda
order	Coleoptera
order	Hemiptera
order	Psocodea
order	Araneae
order	Neuroptera
order	Hymenoptera
order	Thysanoptera
order	Archaeognatha
order	Opiliones
order	Pseudoscorpiones
order	Phasmida
order	Dermaptera
order	Julida
order	Blattodea
order	Lepidoptera
order	Ephemeroptera
order	Trichoptera
order	Lithobiomorpha
order	Geophilomorpha
order	Polydesmida
order	Strepsiptera

Temporal coverage

Data range: 2024-6-11 - 2024-9-27.

Notes: SLAM traps were collected after three months in the studied sites. Pitfall traps were recovered after two weeks (14 nights) of continuous operation.

Collection data

Collection name: Entomoteca Dalberto Teixeira Pombo

Collection identifier: DTP

Specimen preservation method: Ethanol (96%)

Usage licence

Usage licence: Creative Commons Public Domain Waiver (CC-Zero)

Data resources

Data package title: Stratified sampling of Azorean forest arthropods

Resource link: <https://doi.org/10.15468/7aue4t>

Alternative identifiers: <https://www.gbif.org/dataset/d3580ac2-a504-44e0-8e59-de89c430924c>; http://ipt.gbif.pt/ipt/resource?r=azores_forest_arthropods

Number of data sets: 2

Data set name: Event table

Character set: UTF-8

Download URL: http://ipt.gbif.pt/ipt/archive.do?r=azores_forest_arthropods

Data format: Darwin Core Archive format

Data format version: Version 1.6

Description: The dataset was published in the Global Biodiversity Information Facility platform, GBIF (Lhoumeau and Borges 2025). The following data-table includes all the records for which a taxonomic identification of the species was possible. The dataset submitted to GBIF is structured as a sample event dataset that has been published as a Darwin Core Archive (DwCA), which is a standardised format for sharing biodiversity data as a set of one or more data tables. The core data file contains 326 records (eventID). This GBIF IPT (Integrated Publishing Toolkit, Version 2.5.6) archives the data and, thus, serves as the data repository. The data

and resource metadata are available for download in the Portuguese GBIF Portal IPT (Lhoumeau and Borges 2025).

Column label	Column description
id	Unique identification code for sampling event data.
eventID	Identifier of the events, unique for the dataset.
samplingProtocol	The sampling protocol used to capture the species.
sampleSizeValue	The numeric amount of time spent in each sampling.
sampleSizeUnit	The unit of the sample size value.
eventDate	Date or date range the record was collected.
eventRemarks	The verbatim original representation of the date and time information for an Event. In this case, we use the season and year.
habitat	The habitat from which the sample was obtained.
locationID	Identifier of the location.
islandGroup	Name of archipelago, always Azores in the dataset.
island	Name of the island, always Terceira in the dataset.
country	Country of the sampling site, always Portugal in the dataset.
countryCode	ISO code of the country of the sampling site, always PT in the dataset.
stateProvince	Name of the region of the sampling site.
municipality	Municipality of the sampling site.
locality	Name of the locality.
minimumElevationInMetres	The lower limit of the range of elevation (altitude, above sea level), in metres.
locationRemarks	Details on the locality site.
decimalLatitude	Approximate decimal latitude of the trap.
decimalLongitude	Approximate decimal longitude of the trap.
geodeticDatum	The ellipsoid, geodetic datum or spatial reference system (SRS) upon which the geographic coordinates given in decimalLatitude and decimalLongitude are based, always WGS84 in the dataset.
coordinateUncertaintyInMetres	Uncertainty of the coordinates of the centre of the sampling plot.
coordinatePrecision	Precision of the coordinates.
georeferenceSources	A list (concatenated and separated) of maps, gazetteers or other resources used to georeference the Location, described specifically enough to allow anyone in the future to use the same resources.

Data set name: Occurrence table

Character set: UTF-8

Download URL: http://ipt.gbif.pt/ipt/resource?r=azores_forest_arthropods

Data format: Darwin Core Archive format

Data format version: Version 1.6

Description: The dataset was published in the Global Biodiversity Information Facility platform, GBIF (Lhoumeau and Borges 2025). The following data table includes all the records for which a taxonomic identification of the species was possible. The dataset submitted to GBIF is structured as an occurrence table that has been published as a Darwin Core Archive (DwCA), which is a standardised format for sharing biodiversity data as a set of one or more data tables. The core data file contains 2399 records (occurrenceID). This GBIF IPT (Integrated Publishing Toolkit, Version 2.5.6) archives the data and, thus, serves as the data repository. The data and resource metadata are available for download in the Portuguese GBIF Portal IPT (Lhoumeau and Borges 2025).

Column label	Column description
id	Unique identification code for species abundance data. Equivalent here to eventID.
type	The nature or genre of the resource, as defined by the Dublin Core standard. In our case "PhysicalObject".
licence	Reference to the licence under which the record is published.
institutionID	The identity of the institution publishing the data.
collectionID	The identity of the collection where the specimen are conserved.
collectionID	The identity of the collection publishing the data.
institutionCode	The code of the institution publishing the data.
collectionCode	The code of the collection where the specimens are conserved.
datasetName	Name of the dataset.
basisOfRecord	The nature of the data record.
recordedBy	A list (concatenated and separated) of names of peoples, groups or organisations who performed the sampling in the field.
occurrenceID	Identifier of the record, coded as a global unique identifier.
organismQuantity	A number or enumeration value for the quantity of organisms.
organismQuantityType	The type of quantification system used for the quantity of organisms.
sex	The sex and quantity of the individuals captured.

lifeStage	The life stage of the organisms captured.
establishmentMeans	The process of establishment of the species in the location, using a controlled vocabulary: 'native', 'introduced', 'endemic' or 'indeterminate'.
eventID	Identifier of the events, unique for the dataset.
identifiedBy	A list (concatenated and separated) of names of people, groups or organisations who assigned the taxon to the record.
dateIdentified	The date on which the subject was determined as representing the taxon.
scientificName	Complete scientific name including author and year.
kingdom	Kingdom name.
phylum	Phylum name.
class	Class name.
order	Order name.
family	Family name.
genus	Genus name.
specificEpithet	Specific epithet
infraspecificEpithet	Infraspecific epithet.
taxonRank	Lowest taxonomic rank of the record.
scientificNameAuthorship	Name of the author of the lowest taxon rank included in the record.
identificationRemarks	Information about morphospecies identification (code in Dalberto Teixeira Pombo Collection).

Additional information

We collected a total of 32,797 specimens of terrestrial arthropods using SLAM and Pitfall traps deployed across diverse forest strata in native and exotic forests. These specimens, representing the classes Arachnida, Diplopoda, Chilopoda and Insecta, provide a comprehensive snapshot of Azorean arthropod diversity. Of the total collected, 18,372 individuals (56%) were identified at the species or subspecies level — comprising 12,745 adults and 5,627 juveniles (Table 2).

In general, the most abundant order identified was Hemiptera, with 21,939 recorded specimens, underscoring its prevalence in these forest ecosystems. Although not the most abundant, Coleoptera emerged as the most taxonomically diverse group, being represented by 19 distinct families and 50 species and sub-species. The ten most abundant species are predominantly endemic and native non-endemic taxa, with only two introduced species amongst them. This comprehensive dataset significantly augments the existing baseline knowledge on Azorean arthropods and offers valuable

insights into the vertical distribution of species abundance within both native and exotic forests.

Table 2.

Number of individuals sampled and identified at the species or subspecies level.

CAN: canopy layer, UND: understorey layer, GRD: ground layer, EPI: epigean layer.

Epigean layer is sampled with pitfall traps whereas all the other layers are sampled with SLAM traps.

Establishment (species colonisation status) data is according to Borges et al. (2022).

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Arachnida	Araneae	<i>Acorigone acoreensis</i> (Wunderlich, 1992)	endemic	2	17	6	5
Arachnida	Araneae	<i>Agalenatea redii</i> (Scopoli, 1763)	introduced	0	2	0	0
Arachnida	Araneae	<i>Agyneta decora</i> (O. Pickard-Cambridge, 1871)	introduced	2	1	0	0
Arachnida	Araneae	<i>Canariphantes acoreensis</i> (Wunderlich, 1992)	endemic	207	7	0	0
Arachnida	Araneae	<i>Cheiracanthium erraticum</i> (Walckenaer, 1802)	introduced	0	3	1	2
Arachnida	Araneae	<i>Clubiona terrestris</i> Westring, 1851	introduced	0	8	0	0
Arachnida	Araneae	<i>Cryptachaea blattea</i> (Urquhart, 1886)	introduced	0	11	2	0
Arachnida	Araneae	<i>Dysdera crocata</i> C. L. Koch, 1838	introduced	119	18	2	0
Arachnida	Araneae	<i>Erigone atra</i> Blackwall, 1833	introduced	1	0	0	0
Arachnida	Araneae	<i>Erigone dentipalpis</i> (Wider, 1834)	introduced	0	1	0	0
Arachnida	Araneae	<i>Ero furcata</i> (Villers, 1789)	introduced	32	25	10	6
Arachnida	Araneae	<i>Gibbaranea occidentalis</i> Wunderlich, 1989	endemic	2	264	289	280
Arachnida	Araneae	<i>Lasaeola oceanica</i> Simon, 1883	endemic	0	3	0	0
Arachnida	Araneae	<i>Lathys dentichelis</i> (Simon, 1883)	native non-endemic	0	2	0	4
Arachnida	Araneae	<i>Leucognatha acoreensis</i> Wunderlich, 1992	endemic	4	21	27	19
Arachnida	Araneae	<i>Macaroeris cata</i> (Blackwall, 1867)	native non-endemic	0	24	11	15

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Arachnida	Araneae	<i>Macaroeris diligens</i> (Blackwall, 1867)	native non-endemic	0	6	5	11
Arachnida	Araneae	<i>Mangora acalypha</i> (Walckenaer, 1802)	introduced	0	0	0	1
Arachnida	Araneae	<i>Metellina merianae</i> (Scopoli, 1763)	introduced	0	7	0	0
Arachnida	Araneae	<i>Microlinyphia johnsoni</i> (Blackwall, 1859)	native non-endemic	0	84	9	4
Arachnida	Araneae	<i>Ostearius melanopygius</i> (O. Pickard-Cambridge, 1880)	introduced	0	1	0	0
Arachnida	Araneae	<i>Palliduphantes schmitzi</i> (Kulczynski, 1899)	native non-endemic	5	2	1	0
Arachnida	Araneae	<i>Pardosa acorensis</i> Simon, 1883	endemic	5	0	1	1
Arachnida	Araneae	<i>Pisaura acorensis</i> Wunderlich, 1992	endemic	8	26	18	62
Arachnida	Araneae	<i>Porrhoclubiona decora</i> (Blackwall, 1859)	native non-endemic	0	17	2	5
Arachnida	Araneae	<i>Porrhoclubiona genevensis</i> (L. Koch, 1866)	introduced	1	16	0	1
Arachnida	Araneae	<i>Porrhomma borgesii</i> Wunderlich, 2008	endemic	2	0	2	0
Arachnida	Araneae	<i>Rugathodes acorensis</i> Wunderlich, 1992	endemic	12	108	115	27
Arachnida	Araneae	<i>Savigniorhipis acorensis</i> Wunderlich, 1992	endemic	0	73	55	36
Arachnida	Araneae	<i>Segestria florentina</i> (Rossi, 1790)	introduced	0	1	0	0
Arachnida	Araneae	<i>Steatoda nobilis</i> (Thorell, 1875)	native non-endemic	0	1	1	0
Arachnida	Araneae	<i>Tenuiphantes miguelensis</i> (Wunderlich, 1992)	native non-endemic	304	18	1	1
Arachnida	Araneae	<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	introduced	27	45	0	1
Arachnida	Araneae	<i>Theridion melanostictum</i> O. Pickard-Cambridge, 1876	introduced	0	1	0	0
Arachnida	Araneae	<i>Theridion musivivum</i> Schmidt, 1956	native non-endemic	0	4	0	0
Arachnida	Araneae	<i>Walckenaeria grandis</i> (Wunderlich, 1992)	endemic	2	13	0	0
Arachnida	Araneae	<i>Xysticus cor</i> Canestrini, 1873	native non-endemic	0	1	2	5

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Arachnida	Opiliones	<i>Leiobunum blackwalli</i> Meade, 1861	native non-endemic	335	1412	279	174
Arachnida	Pseudoscorpiones	<i>Chthonius ischnocheles</i> (Hermann, 1804)	introduced	26	2	0	0
Arachnida	Pseudoscorpiones	<i>Ephippiochthonius tetrachelatus</i> (Preysler, 1790)	introduced	0	1	0	0
Arachnida	Pseudoscorpiones	<i>Neobisium maroccanum</i> Beier, 1930	introduced	0	8	0	0
Chilopoda	Geophilomorpha	<i>Geophilus truncorum</i> Bergsøe & Meinert, 1866	native non-endemic	1	0	0	0
Chilopoda	Geophilomorpha	<i>Strigamia crassipes</i> (C.L. Koch, 1835)	native non-endemic	2	1	0	0
Chilopoda	Lithobiomorpha	<i>Lithobius pilicornis pilicornis</i> Newport, 1844	native non-endemic	91	1	0	0
Diplopoda	Julida	<i>Blaniulus guttulatus</i> (Fabricius, 1798)	introduced	176	0	0	0
Diplopoda	Julida	<i>Cylindroiulus propinquus</i> (Porat, 1870)	introduced	10	0	0	0
Diplopoda	Julida	<i>Nopoiulus kochii</i> (Gervais, 1847)	introduced	11	1	0	0
Diplopoda	Julida	<i>Ommatoiulus moreleti</i> (Lucas, 1860)	introduced	58	22	7	1
Diplopoda	Julida	<i>Proteroiulus fuscus</i> (Am Stein, 1857)	introduced	3	0	0	0
Diplopoda	Polydesmida	<i>Oxidus gracilis</i> (C.L. Koch, 1847)	introduced	3	0	0	0
Diplopoda	Polydesmida	<i>Polydesmus coriaceus</i> Porat, 1870	introduced	13	0	0	0
Insecta	Archaeognatha	<i>Dilta saxicola</i> (Womersley, 1930)	native non-endemic	0	4	0	2
Insecta	Archaeognatha	<i>Trigoniophthalmus borgesii</i> Mendes, Gaju, Bach & Molero, 2000	endemic	1	160	21	105
Insecta	Blattodea	<i>Zetha simonyi</i> (Krauss, 1892)	native non-endemic	3	142	50	55
Insecta	Coleoptera	<i>Amischa analis</i> (Gravenhorst, 1802)	indeterminate	0	2	0	0
Insecta	Coleoptera	<i>Anaspis proteus</i> Wollaston, 1854	native non-endemic	0	114	74	73
Insecta	Coleoptera	<i>Anisodactylus binotatus</i> (Fabricius, 1787)	introduced	0	0	1	0
Insecta	Coleoptera	<i>Anobium punctatum</i> (De Geer, 1774)	introduced	0	1	0	0
Insecta	Coleoptera	<i>Anotylus nitidifrons</i> (Wollaston, 1871)	indeterminate	270	1	0	0
Insecta	Coleoptera	<i>Atheta fungi</i> (Gravenhorst, 1806)	indeterminate	3	3	0	0

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Insecta	Coleoptera	<i>Atheta pasadenae</i> Bernhauer, 1906	indeterminate	0	1	0	0
Insecta	Coleoptera	<i>Athous azoricus</i> Platia & Gudenzi, 2002	endemic	3	12	0	0
Insecta	Coleoptera	<i>Brassicogethes aeneus</i> (Fabricius, 1775)	introduced	0	1	1	0
Insecta	Coleoptera	<i>Calacalles subcarinatus</i> (Israelson, 1984)	endemic	0	25	12	2
Insecta	Coleoptera	<i>Carpelimus corticinus</i> (Gravenhorst, 1806)	indeterminate	6	8	0	0
Insecta	Coleoptera	<i>Carpelimus troglodytes troglodytes</i> (Erichson, 1840)	indeterminate	2	0	0	0
Insecta	Coleoptera	<i>Cartodere nodifer</i> (Westwood, 1839)	introduced	0	3	0	0
Insecta	Coleoptera	<i>Catops coracinus</i> Kellner, 1846	native non-endemic	1	6	1	0
Insecta	Coleoptera	<i>Cedrorum azoricus azoricus</i> Borges & A.Serrano, 1993	endemic	27	0	0	0
Insecta	Coleoptera	<i>Cephennium validum</i> Assing & Meybohm, 2021	native non-endemic	1	0	0	0
Insecta	Coleoptera	<i>Cercyon haemorrhoidalis</i> (Fabricius, 1775)	introduced	1	0	0	0
Insecta	Coleoptera	<i>Coccinella undecimpunctata undecimpunctata</i> Linnaeus, 1758	introduced	0	1	1	0
Insecta	Coleoptera	<i>Coccotrypes carpophagus</i> (Hornung, 1842)	introduced	0	1	1	0
Insecta	Coleoptera	<i>Creophilus maxillosus maxillosus</i> (Linnaeus, 1758)	indeterminate	0	0	1	0
Insecta	Coleoptera	<i>Cryptamorpha desjardinsii</i> (Guérin-Méneville, 1844)	introduced	0	1	0	1
Insecta	Coleoptera	<i>Drouetius borgesii borgesii</i> (Machado, 2009)	endemic	1	67	3	1
Insecta	Coleoptera	<i>Dryops algericus</i> (Lucas, 1846)	native non-endemic	1	1	1	1
Insecta	Coleoptera	<i>Epitrix hirtipennis</i> (Melsheimer, 1847)	introduced	0	1	0	0
Insecta	Coleoptera	<i>Gonipterus platensis</i> (Marelli, 1926)	introduced	0	2	0	0
Insecta	Coleoptera	<i>Heteroderes azoricus</i> (Tarnier, 1860)	endemic	0	3	0	1
Insecta	Coleoptera	<i>Heteroderes vagus</i> Candèze, 1893	introduced	1	0	0	0

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Insecta	Coleoptera	<i>Kalcapion semivittatum semivittatum</i> (Gyllenhal, 1833)	indeterminate	0	1	0	0
Insecta	Coleoptera	<i>Longitarsus kutscherai</i> (Rye, 1872)	introduced	0	3	0	0
Insecta	Coleoptera	<i>Mecinus pascuorum</i> (Gyllenhal, 1813)	introduced	0	1	2	0
Insecta	Coleoptera	<i>Notothecta dryochares</i> (Israelson, 1985)	endemic	1	52	8	2
Insecta	Coleoptera	<i>Ocypus aethiops</i> (Waltl, 1835)	indeterminate	39	0	0	0
Insecta	Coleoptera	<i>Ocys harpaloides</i> (Audinet-Serville, 1821)	native non-endemic	0	0	5	0
Insecta	Coleoptera	<i>Paranchus albipes</i> (Fabricius, 1796)	introduced	95	0	1	0
Insecta	Coleoptera	<i>Phloeonomus punctipennis</i> Thomson, 1867	indeterminate	1	2	0	0
Insecta	Coleoptera	<i>Phyllotreta striolata</i> (Fabricius, 1803)	introduced	0	0	1	1
Insecta	Coleoptera	<i>Popillia japonica</i> Newman, 1838	introduced	0	4	0	0
Insecta	Coleoptera	<i>Proteinus atomarius</i> Erichson, 1840	indeterminate	2	2	0	0
Insecta	Coleoptera	<i>Pseudoophonus rufipes</i> (De Geer, 1774)	introduced	1	0	0	0
Insecta	Coleoptera	<i>Pseudophloeophagus tenax borgesii</i> Stüben, 2022	endemic	2	74	27	15
Insecta	Coleoptera	<i>Psylliodes marcida</i> (Illiger, 1807)	native non-endemic	0	1	0	0
Insecta	Coleoptera	<i>Sitona discoideus</i> Gyllenhal, 1834	introduced	0	2	0	0
Insecta	Coleoptera	<i>Sphenophorus abbreviatus</i> (Fabricius, 1787)	introduced	1	0	0	0
Insecta	Coleoptera	<i>Stelidota geminata</i> (Say, 1825)	introduced	47	0	1	0
Insecta	Coleoptera	<i>Stilbus testaceus</i> (Panzer, 1797)	native non-endemic	0	1	0	0
Insecta	Coleoptera	<i>Tachyporus chrysomelinus</i> (Linnaeus, 1758)	indeterminate	0	1	0	0
Insecta	Coleoptera	<i>Tachyporus nitidulus</i> (Fabricius, 1781)	indeterminate	1	0	0	0
Insecta	Coleoptera	<i>Tarphius relictus</i> Borges & Serrano, 2017	endemic	3	0	0	0
Insecta	Coleoptera	<i>Trechus terrabravensis</i> Borges, Serrano & Amorim, 2004	endemic	12	0	0	0

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Insecta	Coleoptera	<i>Xyleborinus alni</i> Nijima, 1909	introduced	0	0	1	0
Insecta	Dermaptera	<i>Euborellia annulipes</i> (Lucas, 1847)	introduced	0	6	0	0
Insecta	Dermaptera	<i>Forficula auricularia</i> Linnaeus, 1758	introduced	1	3	0	0
Insecta	Ephemeroptera	<i>Cloeon dipterum</i> (Linnaeus, 1761)	native non-endemic	0	0	1	0
Insecta	Hemiptera	<i>Acalypta parvula</i> (Fallén, 1807)	native non-endemic	0	1	0	0
Insecta	Hemiptera	<i>Acizzia uncatoides</i> (Ferris & Klyver, 1932)	introduced	0	512	82	62
Insecta	Hemiptera	<i>Anthocoris nemoralis</i> (Fabricius, 1794)	native non-endemic	0	1	0	0
Insecta	Hemiptera	<i>Aphrodes hamiltoni</i> Quartau & Borges, 2003	endemic	22	5	0	0
Insecta	Hemiptera	<i>Buchananiella continua</i> (White, 1880)	introduced	0	1	0	0
Insecta	Hemiptera	<i>Campyloneura virgula</i> (Herrich-Schaeffer, 1835)	native non-endemic	1	37	35	17
Insecta	Hemiptera	<i>Cinara juniperi</i> (De Geer, 1773)	native non-endemic	0	90	3	7
Insecta	Hemiptera	<i>Cixius azoterceirae</i> Remane & Asche, 1979	endemic	6	1926	915	1304
Insecta	Hemiptera	<i>Cyphopterum adscendens</i> (Herrich-Schäffer, 1835)	native non-endemic	0	140	73	23
Insecta	Hemiptera	<i>Eupteryx azorica</i> Ribaut, 1941	endemic	0	2	0	2
Insecta	Hemiptera	<i>Eupteryx filicum</i> (Newman, 1853)	native non-endemic	0	20	4	0
Insecta	Hemiptera	<i>Fulvius borgesii</i> Chérot, Ribes & Gorczyca, 2006	introduced	0	0	0	1
Insecta	Hemiptera	<i>Heterotoma planicornis</i> (Pallas, 1772)	native non-endemic	0	1	0	0
Insecta	Hemiptera	<i>Kelisia ribauti</i> Wagner, 1938	native non-endemic	0	10	4	3
Insecta	Hemiptera	<i>Kleidocerys ericae</i> (Horváth, 1909)	native non-endemic	0	329	13	10
Insecta	Hemiptera	<i>Loricula coleoptrata</i> (Fallén, 1807)	native non-endemic	0	4	4	2

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Insecta	Hemiptera	<i>Megamelodes quadrimaculatus</i> (Signoret, 1865)	native non-endemic	43	0	0	1
Insecta	Hemiptera	<i>Monalocoris filicis</i> (Linnaeus, 1758)	native non-endemic	0	112	15	10
Insecta	Hemiptera	<i>Nabis pseudoferus ibericus</i> Remane, 1962	native non-endemic	0	9	4	4
Insecta	Hemiptera	<i>Orius laevigatus laevigatus</i> (Fieber, 1860)	native non-endemic	0	1	0	0
Insecta	Hemiptera	<i>Pilophorus perplexus</i> Douglas & Scott, 1875	native non-endemic	0	0	42	0
Insecta	Hemiptera	<i>Pinalitus oromii</i> J. Ribes, 1992	endemic	0	34	29	48
Insecta	Hemiptera	<i>Rhopalosiphoninus latysiphon</i> (Davidson, 1912)	introduced	10	0	0	0
Insecta	Hemiptera	<i>Saldula palustris</i> (Douglas, 1874)	native non-endemic	0	0	1	1
Insecta	Hemiptera	<i>Scolopostethus decoratus</i> (Hahn, 1833)	native non-endemic	0	0	1	0
Insecta	Hemiptera	<i>Siphanta acuta</i> (Walker, 1851)	introduced	0	85	7	8
Insecta	Hemiptera	<i>Strophingia harteni</i> Hodkinson, 1981	endemic	0	23	6	11
Insecta	Hemiptera	<i>Trioza laurisilvae</i> Hodkinson, 1990	native non-endemic	1	329	376	821
Insecta	Hymenoptera	<i>Hypoponera eduardi</i> (Forel, 1894)	native non-endemic	0	0	1	2
Insecta	Hymenoptera	<i>Lasius grandis</i> Forel, 1909	native non-endemic	52	171	13	20
Insecta	Hymenoptera	<i>Monomorium carbonarium</i> (Smith, 1858)	native non-endemic	0	0	0	3
Insecta	Hymenoptera	<i>Tetramorium caespitum</i> (Linnaeus, 1758)	native non-endemic	0	4	0	0
Insecta	Lepidoptera	<i>Argyresthia atlanticella</i> Rebel, 1940	endemic	4	0	0	0
Insecta	Lepidoptera	<i>Ascotis fortunata azorica</i> Pinker, 1971	endemic	1	0	0	0
Insecta	Lepidoptera	<i>Mythimna unipuncta</i> (Haworth, 1809)	native non-endemic	1	0	0	0
Insecta	Neuroptera	<i>Hemerobius azoricus</i> Tjeder, 1948	endemic	0	64	49	34
Insecta	Phasmida	<i>Carausius morosus</i> (Sinéty, 1901)	introduced	0	3	0	0

Class	Order	Scientific Name	Establishment	EPI	GRD	UND	CAN
Insecta	Psocodea	<i>Atlantopsocus adustus</i> (Hagen, 1865)	native non-endemic	0	14	11	6
Insecta	Psocodea	<i>Bertkauia lucifuga</i> (Rambur, 1842)	native non-endemic	0	16	4	2
Insecta	Psocodea	<i>Ectopsocus briggsi</i> McLachlan, 1899	introduced	2	262	71	104
Insecta	Psocodea	<i>Ectopsocus strauchi</i> Enderlein, 1906	native non-endemic	0	1	1	0
Insecta	Psocodea	<i>Elipsocus azoricus</i> Meinander, 1975	endemic	0	113	68	40
Insecta	Psocodea	<i>Elipsocus brincki</i> Badonnel, 1963	endemic	0	56	37	146
Insecta	Psocodea	<i>Lachesilla greeni</i> (Pearman, 1933)	introduced	0	0	0	2
Insecta	Psocodea	<i>Trichopsocus clarus</i> (Banks, 1908)	native non-endemic	2	307	90	33
Insecta	Psocodea	<i>Valenzuela burmeisteri</i> (Brauer, 1876)	native non-endemic	0	47	17	5
Insecta	Psocodea	<i>Valenzuela flavidus</i> (Stephens, 1836)	native non-endemic	2	1089	266	214
Insecta	Strepsiptera	<i>Elenchus tenuicornis</i> (Kirby, 1815)	native non-endemic	0	0	0	1
Insecta	Thysanoptera	<i>Anisopilothrips venustulus</i> (Priesner, 1923)	introduced	0	1	0	0
Insecta	Thysanoptera	<i>Ceratothrips ericae</i> (Haliday, 1836)	native non-endemic	0	61	13	7
Insecta	Thysanoptera	<i>Heliothrips haemorrhoidalis</i> (Bouché, 1833)	introduced	0	13	2	1
Insecta	Thysanoptera	<i>Hercinothrips bicinctus</i> (Bagnall, 1919)	introduced	0	1	0	0
Insecta	Thysanoptera	<i>Hoplothrips corticis</i> (De Geer, 1773)	native non-endemic	0	65	49	27
Insecta	Trichoptera	<i>Limnephilus atlanticus</i> Nybom, 1948	endemic	7	3	5	0

The dataset provides strong evidence that arthropod communities are structured differently along the vertical gradient in native and exotic forests (Fig. 4). When comparing these two types of forests, we found that distribution of arthropod abundance vary significantly across the three forest strata: ground, understorey and canopy (Table 3).

One of the most striking findings is the more even distribution of arthropods across the vertical strata in native forests compared to exotic forests, where abundance is disproportionately concentrated in the ground layer (Fig. 4).

Table 3.

Pairwise comparisons of adult arthropods abundance between exotic forest and native forest across different strata (EPI: epigean layer, GRD: ground layer, UND: understorey layer, CAN: canopy layer) using Wilcoxon rank sum tests.

The table presents the sample sizes (n1 and n2), test statistic values and significance levels (*p < 0.05, **p < 0.01, ns = not significant) as well as the effect size and magnitude, based on 1000 replications for the significant comparisons.

Strata	Forest type 1	Forest type 2	n1	n2	W	Significance	Effect size	Magnitude
EPI	Exotic forest	Native forest	10	10	62.5	ns	---	---
GRD	Exotic forest	Native forest	10	10	84	**	0.57	large
UND	Exotic forest	Native forest	10	8	15	*	0.52	large
CAN	Exotic forest	Native forest	10	10	9	**	0.69	large

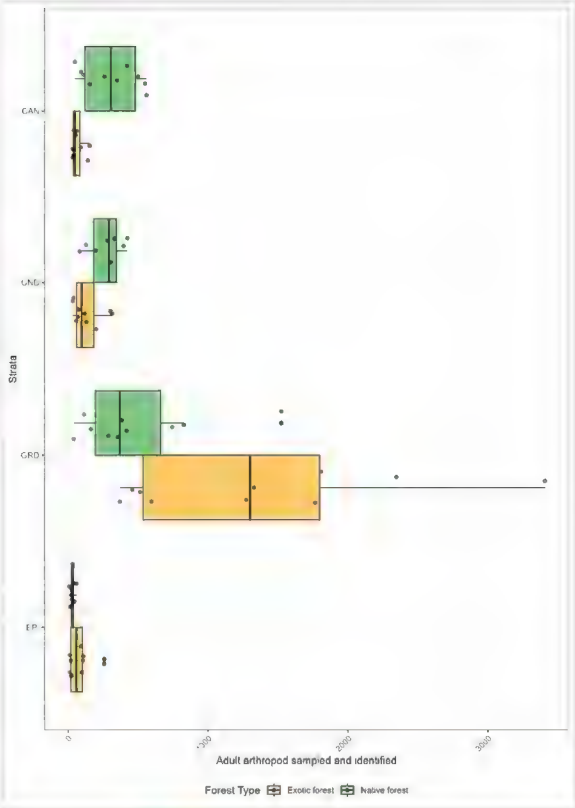


Figure 4. [doi](#)

Abundance of arthropods across different forest strata in exotic and native forests.

The x-axis represents the total number of arthropods collected and identified, while the y-axis indicates the sampled strata (EPI: epigean, GRD: ground, UND: understorey, CAN: canopy). Points represent individual site values for a given forest type. Bars are colour-coded to distinguish between exotic forests (yellow) and native forests (green).

Kruskal-Wallis tests revealed statistically significant differences in adult abundance total across the strata of exotic forest ($\chi^2(3) = 24.2$, $n = 40$, $p < 0.001$) and native forest ($\chi^2(3) = 20.8$, $n = 38$, $p < 0.001$).

In exotic forest, Kruskal-Wallis effect size ($\eta^2[H]$) for the difference in adult abundance total was 0.59 (95% CI [0.35, 0.80], $n = 40$), indicating a large effect. In native forest, the effect was also large with 0.52 (95% CI [0.29, 0.73]).

Native forests offer a greater number of distinct ecological niches at varying heights, thus allowing for a greater degree of vertical partitioning amongst arthropod communities (Basset et al. 2003, Basset et al. 2015, Xing et al. 2023). Therefore, it was hypothesised that the distribution of the overall arthropod assemblage would differ more from one strata to another. However, the observed homogeneity in the abundance distribution could be attributed to the relatively low canopy height within the study plots (Dias et al. 2004, Elias et al. 2016). The well-developed understorey and dense canopy create a structurally complex environment that supports a high diversity of arthropods. The presence of climbing vegetation, epiphytes and diverse leaf architecture contributes to habitat complexity and homogeneity by providing multiple pathway for species to move in the ecosystems. However, when distinguishing the overall arthropod assemblage by order, we detected that native forests are supporting a higher proportion of canopy- and understorey-associated taxa (Fig. 5). Similarly to a study conducted in Amazonian forest by de Souza Amorim et al. (2022), groups such as Araneae, Hemiptera and Hymenoptera (formicidae) show significantly higher relative abundance in the upper strata (Table 4), suggesting that these layers serve as critical habitat for these functional groups (see Arvidsson et al. (2022) on spider's web). The increased presence of predators (e.g. spiders) in the canopy and understorey of native forests may indicate a more complex food web structure, with stronger top-down regulation of herbivore populations (Martinez-Almoyna et al. 2024, Wildermuth et al. 2024).

Table 4.						
Statistical comparison of arthropod order abundance between exotic and native forests across different forest strata (EPI: epigean layer, GRD: ground layer, UND: understorey layer, CAN: canopy layer).						
n1 and n2 represent sample sizes for exotic and native forests, respectively. p-values are derived from statistical tests (Wilcoxon rank sum tests), with significance levels indicated as: ns (not significant), * (p < 0.05), ** (p < 0.01), *** (p < 0.001).						
Order	Strata	n1	n2	W	p-value	Significance
Araneae	EPI	10	10	31	0.162	ns
Araneae	GRD	10	10	19	0.0185	*
Araneae	UND	10	8	2	0.00081	***
Araneae	CAN	10	10	35	0.272	ns
Archaeognatha	EPI	10	10	45	0.368	ns
Archaeognatha	GRD	10	10	31	0.101	ns
Archaeognatha	UND	10	8	25	0.0474	*
Archaeognatha	CAN	10	10	40	0.399	ns
Blattodea	GRD	10	10	42.5	0.572	ns
Blattodea	UND	10	8	20	0.0174	*

Order	Strata	n1	n2	W	p-value	Significance
Blattodea	CAN	10	10	46	0.67	ns
Coleoptera	EPI	10	10	81	0.0211	*
Coleoptera	GRD	10	10	41	0.529	ns
Coleoptera	UND	10	8	68	0.0117	*
Coleoptera	CAN	10	10	100	0.000178	***
Hemiptera	EPI	10	10	5.5	0.00038	***
Hemiptera	GRD	10	10	59	0.529	ns
Hemiptera	UND	10	8	27	0.274	ns
Hemiptera	CAN	10	10	13	0.00578	**
Hymenoptera	EPI	10	10	80	0.00597	**
Hymenoptera	GRD	10	10	59	0.517	ns
Hymenoptera	UND	10	8	39	0.962	ns
Hymenoptera	CAN	10	10	73	0.0626	ns
Julida	EPI	10	10	52	0.901	ns
Julida	GRD	10	10	55	0.69	ns
Julida	UND	10	8	35	0.314	ns
Lithobiomorpha	EPI	10	10	14.5	0.00789	**
Lithobiomorpha	GRD	10	10	45	0.368	ns
Neuroptera	GRD	10	10	51	0.968	ns
Neuroptera	UND	10	8	57	0.138	ns
Neuroptera	CAN	10	10	82	0.0164	*
Opiliones	EPI	10	10	60.5	0.394	ns
Opiliones	GRD	10	10	75	0.062	ns
Opiliones	UND	10	8	37	0.823	ns
Opiliones	CAN	10	10	66.5	0.22	ns
Psocodea	EPI	10	10	65	0.0779	ns
Psocodea	GRD	10	10	54	0.796	ns
Psocodea	UND	10	8	60	0.0831	ns
Psocodea	CAN	10	10	77	0.0433	*
Thysanoptera	GRD	10	10	66	0.238	ns

Order	Strata	n1	n2	W	p-value	Significance
Thysanoptera	UND	10	8	63.5	0.0325	*
Thysanoptera	CAN	10	10	47	0.843	ns

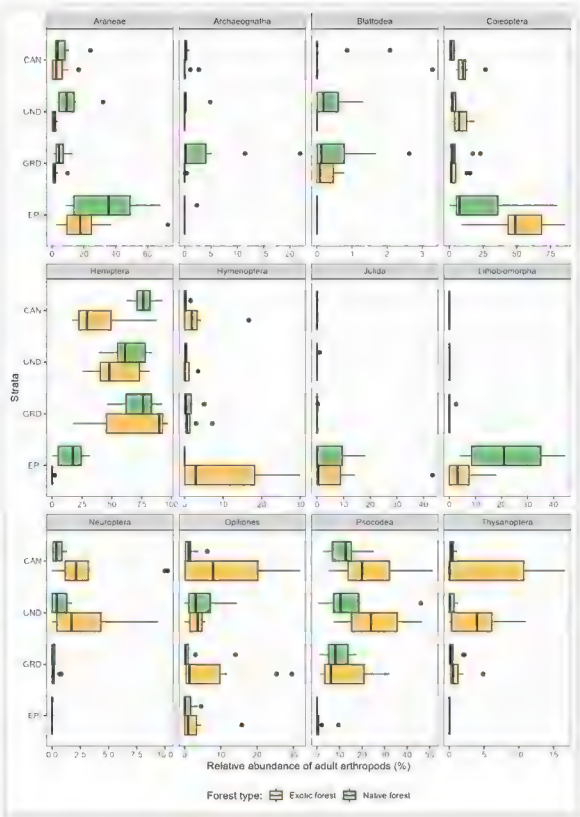


Figure 5. [doi](#)
Arthropod vertical profiles in exotic and native forests for the 12 most abundant order sampled and identified.
Each panel represents the distribution of the relative abundance (%) of a given order to the total number of individuals sampled in a forest strata (EPI: epigean, GRD: ground, UND: understorey, CAN: canopy) of exotic forests (yellow) and native forests (green).

In the Azores, exotic forests are dominated by fast-growing, homogeneous tree species and lack the complex understorey and dense canopy of native forests (Connor et al. 2012, Borges Silva et al. 2017, Borges Silva et al. 2018). It is hypothesised that the combination of elevated canopy height and an absence of vertically structural elements may lead to a heightened degree of microclimatic differentiation, which, in turn, may result in a more pronounced vertical stratification within arthropod communities. Additionally, arthropod abundance is significantly higher in the ground layer of exotic forests compared to native forests (Table 3), suggesting that these simplified forest structures concentrate arthropod activity near the forest floor. Many arthropod orders, including detritivores (Julida, Lithobiomorpha) and scavengers (Psocoptera), concentrated in the ground layer (Fig. 5). The significantly higher abundance of these groups in the lower strata (Table 4) suggests that exotic forests may be more reliant on decomposition-based energy pathways rather than complex trophic interactions involving arboreal predators and herbivores. This shift could have important implications for ecosystem functioning, potentially leading to altered nutrient cycling and reduced ecological resilience. In addition, the number of specimens sampled from the ground layer in exotic forests might be link to the invasion pattern

previously documented by Cardoso et al. (2007), where most of the species appeared to be non-indigenous in this ecosystem.

Overall, our study present, for the first time, a comprehensive stratified survey of forest arthropods in two different forest ecosystem in the Azores Archipelago. The significant differences observed in both overall abundance and order-level composition across strata provide strong evidence that these two forest type are not ecologically equivalent highlighting the need to preserve native forests and enhance vertical complexity in exotic forest to sustain arthropod biodiversity and ecosystem services in forested landscapes. Additionally, future studies should assess how forest structure, microclimatic conditions and resource availability shape arthropod vertical distribution.

Acknowledgements

This study was only possible due to the financial support of several projects for acquiring the SLAM traps, namely:

Portal da Biodiversidade dos Açores (2022-2023) - PO Azores Project - M1.1.A/INFRAEST CIENT/001/2022;

FCT-UIDB/00329/2020-2024 (Thematic Line 1 – integrated ecological assessment of environmental change on biodiversity) (2019-2024);

Science and Technology Foundation (FCT) - MACRISK-Trait-based prediction of extinction risk and invasiveness for Northern Macaronesian arthropods (FCT-PTDC/BIA-CBI/0625/2021).

SL was supported by the PhD Grant "The impact of habitat structure change on arthropod food web complexity in Azorean forests" (PhD grant M3.1.a/F/012/2022).

Open access was funded by the project FCT-UID/00329/2025, Centre for Ecology, Evolution and Environmental Changes (CE3C).

Author contributions

SL: Conceptualisation; Research (field and laboratory work); Data Curation; Darwin Core dataset preparation; Formal analysis and interpretation; manuscript writing and revision.

PAVB: Conceptualisation; Methodology; Research (field and laboratory work); Resources; Data Curation; Darwin Core dataset preparation; Formal analysis and interpretation; manuscript writing and revision.

AL: Laboratory work, manuscript revision.

All the remaining authors participated in research (field and laboratory work) and manuscript revision.

References

- Arvidsson F, Montes M, Birkhofer K (2022) Microhabitat conditions affect web-building spider communities and their prey independent of effects of short-term wildlife fencing on forest vegetation. *The Journal of Arachnology* 50 (3). <https://doi.org/10.1636/joa-s-21-046>
- Basham E, Baecher JA, Klings D, Scheffers B (2023) Vertical stratification patterns of tropical forest vertebrates: a meta-analysis. *Biological Reviews* 98 (1): 99-114. <https://doi.org/10.1111/brv.12896>
- Basset Y, Hammond P, Barrios H, Holloway J, Miller S (2003) Vertical stratification of arthropod assemblages. In: Basset Y, Novotny V, Miller S, Kitching R (Eds) *Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, 492 pp. [ISBN 978-0-521-82000-4].
- Basset Y, Cizek L, Cuénoud P, Didham R, Novotny V, Ødegaard F, Roslin T, Tishechkin A, Schmidl J, Winchester N, Roubik D, Aberlenc H, Bail J, Barrios H, Bridle J, Castaño-Meneses G, Corbara B, Curletti G, Duarte da Rocha W, De Bakker D, Delabie JC, Dejean A, Fagan L, Floren A, Kitching R, Medianero E, Gama de Oliveira E, Orivel J, Pollet M, Rapp M, Ribeiro S, Roisin Y, Schmidt J, Sørensen L, Lewinsohn T, Leponce M (2015) Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. *PLOS One* 10 (12). <https://doi.org/10.1371/journal.pone.0144110>
- Borges PAV, Pimentel R, Carvalho R, Nunes R, Wallon S, Ros-Prieto A (2017) Seasonal dynamics of arthropods in the humid native forests of Terceira Island (Azores). *Arquipelago-Life and Marine Sciences* 34: 105-122. URL: <chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://www.maiisg.com/fotos/publicacoes/1504696284.pdf>
- Borges PAV, Rigal F, Ros-Prieto A, Cardoso P (2020) Increase of insular exotic arthropod diversity is a fundamental dimension of the current biodiversity crisis. *Insect Conservation and Diversity* 13 (5): 508-518. <https://doi.org/10.1111/icad.12431>
- Borges PAV, Lamelas-Lopez L, Andrade R, Lhoumeau S, Vieira V, Soares AO, Borges I, Boieiro M, Cardoso P, Crespo LC, Karsholt O, Schülke M, Serrano ARM, Quartau JA, Assing V (2022) An updated checklist of Azorean arthropods (Arthropoda). *Biodiversity Data Journal* 10: e97682. <https://doi.org/10.3897/BDJ.10.e97682>
- Borges Silva L, Teixeira A, Alves M, Elias RB, Silva L (2017) Tree age determination in the widespread woody plant invader *Pittosporum undulatum*. *Forest Ecology and Management* 400: 457-467. <https://doi.org/10.1016/j.foreco.2017.06.027>
- Borges Silva L, Lourenço P, Teixeira A, Azevedo EB, Alves M, Elias RB, Silva L (2018) Biomass valorization in the management of woody plant invaders: The case of *Pittosporum undulatum* in the Azores. *Biomass and Bioenergy* 109: 155-165. <https://doi.org/10.1016/j.biombioe.2017.12.025>
- Borges Silva L, Pavão D, Elias RB, Moura M, Ventura MA, Silva L (2022) Taxonomic, structural diversity and carbon stocks in a gradient of island forests. *Scientific Reports* 12 (1). <https://doi.org/10.1038/s41598-022-05045-w>
- Cardoso P, Borges PAV, Gaspar C (2007) Biotic integrity of the arthropod communities in the natural forests of Azores. *Biodiversity and Conservation* 16 (10): 2883-2901. <https://doi.org/10.1007/s10531-006-9078-x>
- Cardoso P, Barton P, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima C, Gaigher R, Habel J, Hallmann C, Hill M, Hochkirch A, Kwak M, Mammola S, Ari Noriega

- J, Orfinger A, Pedraza F, Pryke J, Roque F, Settele J, Simaika J, Stork N, Suhling F, Vorster C, Samways M (2020) Scientists' warning to humanity on insect extinctions. *Biological Conservation* 242 <https://doi.org/10.1016/j.biocon.2020.108426>
- Cardoso P, Pekar S, Birkhofer K, Chuang A, Fukushima CS, Hebets EA, Henaut Y, Hesselberg T, Malumbres-Olarte J, Michálek O, Michalko R, Scott C, Wolff J, Mammola S (2024) Ecosystem services provided by spiders. Preprints. <https://doi.org/10.22541/au.172538631.11011603/v1>
 - Chen J, Saunders S, Crow T, Naiman R, Brosfokske K, Mroz G, Brookshire B, Franklin J (1999) Microclimate in Forest Ecosystem and Landscape Ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience* 49 (4): 288-297. <https://doi.org/10.2307/1313612>
 - Connor S, van Leeuwen JN, Rittenour T, van der Knaap W, Ammann B, Björck S (2012) The ecological impact of oceanic island colonization – a palaeoecological perspective from the Azores. *Journal of Biogeography* 39 (6): 1007-1023. <https://doi.org/10.1111/j.1365-2699.2011.02671.x>
 - Costa R, Cardoso P, Rigal F, Borges PAV (2023) Island spider origins show complex vertical stratification patterns in Macaronesia. *Insect Conservation and Diversity* 16 (6): 886-895. <https://doi.org/10.1111/icad.12686>
 - De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers B, Hylander K, Luoto M, Vellend M, Verheyen K, Lenoir J (2019) Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution* 3 (5): 744-749. <https://doi.org/10.1038/s41559-019-0842-1>
 - de Souza Amorim D, Brown B, Boscolo D, Ale-Rocha R, Alvarez-Garcia DM, Balbi MA, de Marco Barbosa A, Capellari RS, de Carvalho CJB, Couri MS, de Vilhena Perez Dios R, Fachin DA, Ferro G, Flores HF, Frare LM, Gudín FM, Hauser M, Lamas CJE, Lindsay K, Marinho MAT, Marques DWA, Marshall S, Mello-Patiu C, Menezes MA, Morales MN, Nihei S, Oliveira SS, Pirani G, Ribeiro GC, Riccardi PR, de Santis MD, Santos D, dos Santos JR, Silva VC, Wood EM, Rafael JA (2022) Vertical stratification of insect abundance and species richness in an Amazonian tropical forest. *Scientific Reports* 12 (1). <https://doi.org/10.1038/s41598-022-05677-y>
 - Dias E, Elias RB, Nunes V (2004) Vegetation mapping and nature conservation: a case study in Terceira Island (Azores). *Biodiversity & Conservation* 13 (8): 1519-1539. <https://doi.org/10.1023/B:BIOC.0000021326.50170.66>
 - Ehbrecht M, Seidel D, Annighöfer P, Kreft H, Köhler M, Zemp DC, Puettmann K, Nilus R, Babweteera F, Willim K, Stiers M, Soto D, Boehmer HJ, Fisichelli N, Burnett M, Juday G, Stephens S, Ammer C (2021) Global patterns and climatic controls of forest structural complexity. *Nature Communications* 12 (1). <https://doi.org/10.1038/s41467-020-20767-z>
 - Elias RB, Gil A, Silva L, Fernández-Palacios JM, Azevedo EBd, Reis F (2016) Natural zonal vegetation of the Azores Islands: characterization and potential distribution. *Phytocoenologia* 46 (2): 107-123. <https://doi.org/10.1127/phyto/2016/0132>
 - Fernández-Palacios JM, Kreft H, Irl SH, Norder S, Ah-Peng C, Borges PV, Burns K, de Nascimento L, Meyer J, Montes E, Drake D (2021) Scientists' warning – The outstanding biodiversity of islands is in peril. *Global Ecology and Conservation* 31 <https://doi.org/10.1016/j.gecco.2021.e01847>
 - Florencio M, Patiño J, Nogué S, Traveset A, Borges PAV, Schaefer H, Amorim IR, Arnedo M, Ávila SP, Cardoso P, de Nascimento L, Fernández-Palacios JM, Gabriel SI, Gil A, Gonçalves V, Haroun R, Illera JC, López-Darias M, Martínez A, Martins GM, Neto AI,

- Nogales M, Oromí P, Rando JC, Raposeiro PM, Rigal F, Romeiras MM, Silva L, Valido A, Vanderpoorten A, Vasconcelos R, Santos AMC (2021) Macaronesia as a Fruitful Arena for Ecology, Evolution, and Conservation Biology. *Frontiers in Ecology and Evolution* 9 (718169). <https://doi.org/10.3389/fevo.2021.718169>
- Gillespie R, Roderick G (2002) Arthropods on Islands: Colonization, Speciation, and Conservation. *Annual Review of Entomology* 47 (Volume 47, 2002): 595-632. <https://doi.org/10.1146/annurev.ento.47.091201.145244>
 - Kondraskov P, Schütz N, Schüßler C, Sequeira MMd, Guerra AS, Caujapé-Castells J, Jaén-Molina R, Marrero-Rodríguez Á, Koch M, Linder P, Kovar-Eder J, Thiv M (2015) Biogeography of Mediterranean hotspot biodiversity: Re-evaluating the 'Tertiary Relict' hypothesis of Macaronesian laurel forests. *PLOS One* 10 (7). <https://doi.org/10.1371/journal.pone.0132091>
 - Laurans M, Hérault B, Vieilledent G, Vincent G (2014) Vertical stratification reduces competition for light in dense tropical forests. *Forest Ecology and Management* 329: 79-88. <https://doi.org/10.1016/j.foreco.2014.05.059>
 - Lhoumeau S, Borges PAV (2023) Assessing the impact of insect decline in Islands: Exploring the diversity and community patterns of indigenous and non-indigenous arthropods in the Azores native forest over 10 Years. *Diversity* 15 (6). <https://doi.org/10.3390/d15060753>
 - Lhoumeau S, Borges PAV (2025) Stratified sampling of Azorean forest arthropods. *Global Biodiversity Information Facilities*. version 1.6. <https://doi.org/10.15468/7AUE4T>
 - Martinez-Almoyna C, Calderón-Sanou I, Lionnet C, Gielly L, Boyer F, Dufour P, Dunyach L, Miquel C, Ohlmann M, Poulenard J, Renaud J, Saillard A, Si-Moussi S, Stephan R, Varoux M, The Orchamp Consortium, Münkemüller T, Thuiller W (2024) Vegetation structure and climate shape mountain arthropod distributions across trophic levels. *Journal of Animal Ecology* 93 (10): 1510-1523. <https://doi.org/10.1111/1365-2656.14164>
 - Matthews TJ, Sadler J, Carvalho R, Nunes R, Borges PAV (2019) Differential temporal beta-diversity patterns of native and non-native arthropod species in a fragmented native forest landscape. *Ecography* 42 (1): 45-54. <https://doi.org/10.1111/ecog.03812>
 - Mueller-Dombois D (1992) The formation of island ecosystems. *GeoJournal* 28 (2). <https://doi.org/10.1007/BF00177244>
 - Oliveira B, Scheffers B (2019) Vertical stratification influences global patterns of biodiversity. *Ecography* 42 (2): 249-249. <https://doi.org/10.1111/ecog.03636>
 - OpenTopography (2013) Shuttle Radar Topography Mission (SRTM) Global. OpenTopography. <https://doi.org/10.5069/G9445JDF>
 - Pan Y, Birdsey R, Phillips O, Jackson R (2013) The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics* 44 (Volume 44, 2013): 593-622. <https://doi.org/10.1146/annurev-ecolsys-110512-135914>
 - Thiel S, Tschapka M, Heymann E, Heer K (2021) Vertical stratification of seed-dispersing vertebrate communities and their interactions with plants in tropical forests. *Biological Reviews* 96 (2): 454-469. <https://doi.org/10.1111/brv.12664>
 - Tsafack N, Lhoumeau S, Ros-Prieto A, Navarro L, Kocsis T, Manso S, Figueiredo T, Teresa Ferreira M, Borges PAV (2023) Arthropod-based biotic integrity indices: A novel tool for evaluating the ecological condition of native forests in the Azores archipelago. *Ecological Indicators* 154 <https://doi.org/10.1016/j.ecolind.2023.110592>
 - UNEP-WCMC (2025) Protected area profile for Portugal from the World Database on Protected Areas. URL: www.protectedplanet.net

- Wildermuth B, Penanhoat A, Sennhenn-Reulen H, Matevski D, Drescher J, Aubry-Kientz M, Seidel D, Schuldt A (2024) Canopy structure influences arthropod communities within and beyond tree identity effects: Insights from combining LiDAR data, insecticidal fogging and machine learning regression modelling. *Ecological Indicators* 160 <https://doi.org/10.1016/j.ecolind.2024.111901>
- Wong ML, Guénard B, Lewis O (2019) Trait-based ecology of terrestrial arthropods. *Biological Reviews* 94 (3): 999-1022. <https://doi.org/10.1111/brv.12488>
- Xing S, Leahy L, Ashton L, Kitching R, Bonebrake T, Scheffers B (2023) Ecological patterns and processes in the vertical dimension of terrestrial ecosystems. *Journal of Animal Ecology* 92 (3): 538-551. <https://doi.org/10.1111/1365-2656.13881>